

STAMINATE STROBILUS OF *TAXUS CANADENSIS*

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 255

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(WITH PLATES XXIV-XXVI AND TWENTY-TWO FIGURES)

Introduction

In a previous paper (8) the writer described the gametophytes of *Taxus canadensis* Marsh., with the statement that other phases of the morphology would be treated in later papers. In this paper the staminate structures with respect to development and vascular anatomy are described. The lack of detailed information concerning these structures has seemed to the writer sufficient justification for the investigation here reported. In view of the generally recognized conservative character of the staminate structures in conifers, it seems that a more extended investigation of them, in the group as a whole, would be worth while. The description of the ovulate structures will be given in another paper.

The general statement in the previous paper as to material and methods will also apply here. The writer is under obligations to Professor W. L. EIKENBERRY, of the University of Kansas, for some material collected in northern Illinois a number of years ago. Acknowledgments are also due Professors JOHN M. COULTER and C. J. CHAMBERLAIN, under whose direction the study of *Taxus canadensis* was begun.

Historical

While the male gametophyte and its attendant features have received considerable attention, apart from the general more obvious features very little is found in the literature dealing with *Taxus* as to the morphology of the staminate strobilus itself. The earlier workers who studied the staminate structures of conifers were concerned largely in attempts to interpret them in terms of the angiosperm flower, naturally leading to confusion as to the true nature of the structures. These earlier views have been summarized by VON MOHL (26) in perhaps one of the most important

of the early papers dealing with the "male flowers" of conifers, and to which we are indebted for part of the following statement regarding this early interpretation of the staminate strobilus of *Taxus*.

LINNAEUS (16) regarded the entire strobilus as a single flower, with the stamens in a cylinder, the perianth lacking and replaced by bud scales. JUSSIEU (13) held that the strobilus was a monadelphous flower; while LINDLEY (15) considered the strobilus as a true cone with naked monadelphous flowers, each sporophyll representing a flower. RICHARD (19) went still farther, with the rather unique view that there were 5-8 flowers under each scale to which the stalk of the flower is attached on the underside. According to this view the pollen sac represented a "flower," and he had a similar interpretation for the sporophylls of *Thuja* and *Juniperus*. ZUCCARINI (28), regarding the reproductive structures as modified portions of the stem, comparable with the phylloclads of *Phyllocladus*, described the anther of *Taxus* as 7-8-lobed around the tip of a central column. He considered that *Taxus* has the most complete male flower in conifers, in other forms the anther folds growing on only one side of the central column, the other side growing out into a scale. VON MOHL opposes the idea of the stem character of the "flower" of conifers, and objects to the view that the "anthers" of other conifers have been derived from such a structure as that of *Taxus*, because "we have yet no certain data with which we can determine with certainty whether the anther of *Taxus* arises from one leaf or from a whorl of leaves."

As compared with our present ideas these early views are rather strange, having largely only a historical interest, with very little bearing on the real morphology of the structures concerned. Considerably later STRASBURGER (22) made some observations on *T. baccata*, describing the spiral arrangement of the scales of the strobilus and the grosser features of the development of the sporophylls. He held that the peltate stamen of *Taxus* represents the "extreme form of stamen," and found that it begins as a rounded knob about the first of August, becomes lobed by lateral swellings due to internal growth, and that pollen mother cells form in these lateral swellings and produce pollen by tetrad divisions. He also describes the pollen region as separated from the epidermis by two

layers of irregular cells, and states that dehiscence is accomplished by the rupture of cells at the base and sides of the pollen sac. CHAMBERLAIN (3) describes the microsporangium of *T. canadensis* at the mother cell stage (October 1, 1897), at which time the nuclei are still rather small in comparison with the size of the cell, the tapetum being sharply differentiated, and its cells showing no tendency to plasmolyze like the cells of the sporangium wall. PILGER (18) describes the general external features, largely from the taxonomic viewpoint, speaking of the "flower" as consisting only of sporophylls surrounded at the base by a scale envelope which completely incloses the flower in the bud state. He regards the "leafy structure" of the anther, which is yet to be recognized in *Torreya* and *Cephalotaxus*, as being "entirely lost" in *Taxus*.

In the related forms the staminate structures of *Torreya* have been described in a general way by PILGER, based on *T. nucifera*; in more detail by Miss ROBERTSON (20) for *T. californica*; and by COULTER and LAND (5) for *T. taxifolia*. In *Cephalotaxus* some of the features of the spermatogenesis have been described by STRASBURGER (23), and by ARNOLDI (1). STRASBURGER (24) pointed out that the pollen grain divides in the sporangium before shedding; LAWSON (14) also confirms this in *C. drupacea*; and WORSDELL (27) gives a description of the general features of the "male flower," based on *C. Fortunei*, comparing it with those of other forms (*Phyllocladus* and *Ginkgo*), especially in the sporophyll features.

Strobili buds

In the axils of the leaves of the shoot of a given season 3 types of structures are produced: (1) the vegetative buds from which develop the lateral leafy shoots of the next season; (2) the young staminate structures, maturing the next season; and (3) the ovule-bearing structures, also maturing the next season. During the first season all of these structures are in bud form, the staminate buds during the latter part of the summer and winter being more globular than the other two kinds, which are so nearly alike in external appearance as to make their distinction uncertain except by very careful examination.

The rudiments of these structures begin to develop very soon after the beginning of growth of the terminal bud in the spring, the



FIGS. 1-6.—Longitudinal sections of young buds: fig. 1, young vegetative shoot with bud rudiment in axil of young leaf; fig. 2, vegetative bud with conical apex; fig. 3, staminate bud with broadened apex; fig. 4, ovulate bud, showing vegetative tip (to left) and rudiment of ovulate strobilus in axil of scale; fig. 5, young staminate strobilus, showing primordia of stamens and tip of axis; fig. 6, young staminate strobilus with primordia of sporophylls, axis apex not evident; $\times 36$.

rudiments appearing as conical projections in the axils of young leaves (fig. 1). By the middle of June these axillary structures have

attained a length averaging about 1.5 mm., consisting of the main axis surrounded by compactly arranged scales. In this early stage one cannot distinguish these structures from one another, either by external appearance or in section. Early in July, however, one can recognize in median longitudinal sections the beginning of the differentiation which is now taking place, the apex of the vegetative bud remaining conical (fig. 2), as is characteristic of the vegetative stem tip (fig. 1), the apex of the staminate structure becoming broadened (fig. 3), while the ovule-bearing structure is recognizable by the rudiment of the ovulate strobilus appearing in the axil of one of the scales near the tip of the primary shoot (fig. 4). All 3 kinds of buds may occur on the same shoot; in fact, this is the usual occurrence, with the staminate buds generally the more numerous, the vegetative buds nearest the tip, and one to several ovulate buds a short distance below the vegetative ones, the staminate buds occupying the older portion of the shoot.

The buds arise only on the current season's growth, and in case of the staminate structures always mature the next season. No cases were observed in which staminate strobili were produced on older growth, nor were any cases found in which the buds remain dormant for a time and then mature. Miss ROBERTSON, in her study of *Torreya californica* from trees growing in England, found that while the staminate strobili are formed in the axils of the leaves of a current season, they may remain dormant for as long as 3 years. In *Taxus* buds may be found on older growth, but they are either dormant vegetative buds or persisting primary shoots of the ovuliferous structures of a former season, as will be described more fully in the paper dealing with these structures.

Sporophylls

PRIMORDIA

The broadened apex (fig. 3) is the first indication of the true nature of the staminate strobilus bud, and can be recognized first about July 1. STRASBURGER (22) was able to recognize the staminate structure of *T. baccata* about August 1, and in *Torreya taxifolia* COULTER and LAND (5) first observed the staminate buds in July,

but the primordia of the sporophylls did not begin to appear until August. The greater meristematic activity in some regions of this rounded apex than in others marks the position of the primordia of the sporophylls. These soon become rounded lobes above the general surface (figs. 5, 6). The nature of the growth of the primordium would indicate that it arises from a group of meristematic cells rather than from a definite initial; at least no defined sporophyll initial could be recognized.

The sporophylls are probably spirally arranged, although this is somewhat indefinite, and indications were found in a few cases that they may arise in acropetal succession (fig. 5); but if this is the case it is very soon obscured in the uniform development of the primordia as the sporophylls develop, no trace of the axis apex being recognizable after the very early beginnings of the sporophylls. The early development of the primordium is uniform in all directions from its central axis, at least until the differentiation of the archesporial initials takes place. The strobilus in this stage shows a series of rounded sporophyll primordia (figs. 5, 6, 23). The later development of the sporophyll is so intimately bound up with the development of the sporangia as to best be described in connection with them. In fact, the development of the sporangia determines the shape and character of the sporophyll, as aside from the sporangia the sporophyll consists of practically nothing excepting the short central axis and the epidermis.

MICROSPORANGIUM

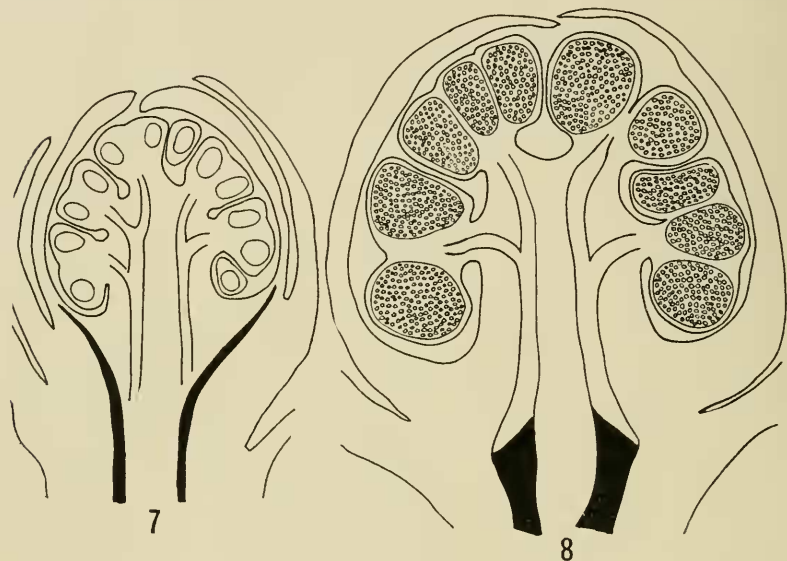
ARCHESPORIAL INITIALS.—HOFMEISTER (11) seems to have been the first to publish with reference to the microsporangium of conifers, reporting the spore mother cell stage as being reached in *Pinus maritima* in November. GOEBEL (9) traced the archesporium of *Pinus* to a single hypodermal cell, and claimed a similar origin for the archesporium of *Thuja*. His most important observation on this point was that the development of the microsporangium is like that of the eusporangiate ferns. COKER (4) in *Taxodium distichum*, and NICHOLS (17) in *Juniperus communis* var. *depressa*, also found a hypodermal origin of the archesporium, in the latter case consisting of “a plate of radially elongated cells, 4-6 in

number, when viewed in longitudinal section.” COULTER and LAND, interpreting the structures in abortive sporangia, conclude that in *Torreya taxifolia* there is “a single hypodermal archesporial cell.” Miss ROBERTSON did not get the origin of the sporogenous tissue in *T. californica*.

In *Taxus canadensis* the development follows the usual eu-sporangiate method, the 4-8 (usually 5-7) archesporial initials arising from the hypodermal layer of the sporophyll primordium while this structure is yet quite small (fig. 23), being uniformly distributed along its margin, and, dividing by periclinal walls, form the primary wall cell and the primary sporogenous cell (figs. 27-29), as in *Torreya taxifolia* (5) and most other forms. These initials are first to be recognized by the size of the cells and of their nuclei (figs. 23-26). One initial cell seems to be the rule, although cases were found in which the archesporium consists of 2 cells (fig. 26).

SPOROGENOUS TISSUE.—The primary sporogenous cell or cells soon divide periclinally (fig. 30) or anticlinally before or after the division of the primary wall cell, and by successive divisions the mass of the sporogenous cells is increased (figs. 31-35), the formation and growth of which result in the lobed peltate structure of the sporophyll, the sporangia being uniformly distributed around the central axis which continues the very short stalk of the sporophyll. As the tissue increases there is a corresponding growth of the epidermis and the sporangium wall (to be described later), the completion of which results in the separation of the sporogenous tissue from the other portion of the sporophyll (fig. 34). The tapetum is differentiated from the peripheral layer, and the remaining sporogenous mass increases in amount until the mother cell stage is reached early in October, as described by CHAMBERLAIN (3) and the writer (8). This has been given (6), and even quite recently (7), as the winter condition of the microsporangium, and has frequently been quoted by writers. As the author has already pointed out (8), microspore formation takes place during the early part of October, collections covering a number of years and from several localities in the northern United States bearing out the statement that the microspore is the winter condition of *Taxus canadensis*. STRASBURGER (25) found microspore formation in *T. baccata* taking place

in February in 1904, during unusually warm weather, indicating that in this form the sporogenous tissue remains in the mother cell stage until spring. It would be of interest to know the behavior in the extreme northern part of the range of *T. canadensis*, as it is possible that in regions farther to the north the microspore stage might not be reached before winter. The microspore mother cell stage is the winter condition of *Torreya californica* (20) in England



FIGS. 7, 8.—Median longitudinal sections of older strobili: fig. 7, at time of completion of sporangium wall, showing oval areas of young sporogenous tissue; vascular tissue of axis and upper scales, shown in black, embryonic vascular tissue of upper portion in outline; fig. 8, winter condition of strobilus, showing globular character of bud and microspores; vascular tissue as in preceding figure; $\times 36$.

and of *T. taxifolia* (5) in Florida. During this development the strobilus has grown considerably in size (cf. figs. 7 and 8), becoming more pronouncedly globular, and it remains in this condition until the renewed growth of spring takes place.

No cases of abortive sporangia were found, and it seems a safe assumption that a sporangium develops from each initial or initial group. The adult sporangia show some variation in size, but not enough to indicate any tendency to abortion of any of them. This

is in marked contrast with the behavior in the related *Torreya*, in which a resin cavity results from the abortion of some of the potentially sporogenous tissue of the sporophyll, the abortion beginning at the primary sporogenous cell stage, as pointed out by COULTER and LAND for *T. taxifolia*. This results in the sporangia occurring on only one side of the otherwise peltate sporophyll. Miss ROBERTSON also finds that normally there are 4 sporangia on the side of the sporophyll of *T. californica* and a resin cavity on the other side, but that the strobilus axis sometimes terminates in a radially symmetrical sporophyll, like that of *Taxus*, with 6 or 7 mature sporangia. Whether a resin cavity is present in such a sporophyll is not stated, the inference being that most or all of the sporangium initials reached maturity. A similar abortion of sporangia, in the formation of mucilage cavities, is indicated by Miss STARR'S (21) work on *Ginkgo biloba*. COULTER and LAND find in *Pinus Laricio* resin cavities related to sporangia, exactly as are the lateral sporangia to the two middle ones in *Torreya*, and say "there is evident a tendency to reduce the number of sporangia by abortion, a reduction that has proceeded farther in *Pinus* than in *Torreya*, and in the latter farther than in *Taxus*." It seems that when resin or mucilage cavities are present in the sporophyll the sporangium initials are involved, and when absent these initials may all function normally, as in *Taxus*. Whether this can be made as a general statement for all forms with resin cavities in the sporophyll must wait for more extensive work on other forms. *Cephalotaxus* has a sporophyll similar in general appearance to that of *Torreya*, but it is not known whether any abortion takes place.

SPORANGIUM WALL.—The initial development of the wall is from the primary wall cell, which by a periclinal division forms a tier of 2 cells. As the sporogenous tissue develops, these wall cells divide anticlinally (fig. 31), increasing the extent of the wall layers. Only a portion of the wall is derived from the primary wall cell, however, as other cells abutting the young sporogenous tissue divide periclinally and add to the wall, first on the outer side (figs. 31-33) and then on the inner side as well (fig. 34), thus completely enveloping the young sporogenous tissue. The wall usually consists of 2 layers of cells, although 3 or even more layers may be present,

especially at the angles formed by the mutual pressure of the sporangial lobes.

As the sporogenous tissue increases in size there is pressure upon the wall cells, and they become flattened and extended, so that at the time of their maximum development they are broad thin plates. By the time of spore formation they are usually quite flattened (fig. 36), and during the further growth of the spores become more or less disorganized, so that by the time the spores have reached maturity, just before shedding, the wall has become a very thin layer abutting the epidermis, which has now become, in effect, the functional sporangium wall.

TAPETUM.—At the time when the sporangium wall is completed the sporogenous tissue inclosed within it is uniform in appearance (fig. 34). Soon, however, the peripheral layer of this tissue becomes differentiated as a tapetum (fig. 35), thus originating from the sporogenous tissue and not from the inner layer of the sporangium wall, as in some forms. The tapetum, however, has its chief significance from a physiological standpoint, being generally regarded as a nutritive layer, its origin seeming to be of little morphological significance. The tapetal cells are usually uninucleate, but not infrequently are binucleate (figs. 35–36). The tapetum is quite distinct during later phases of the development of the sporogenous tissue, is sharply differentiated at the spore mother cell stage, as pointed out by CHAMBERLAIN (3), and remains distinct during the early winter (fig. 36). With the growth of the microspores in the spring it becomes less and less prominent, until near pollination it consists of only a very thin layer of disorganized material surrounding the spore mass.

EPIDERMIS

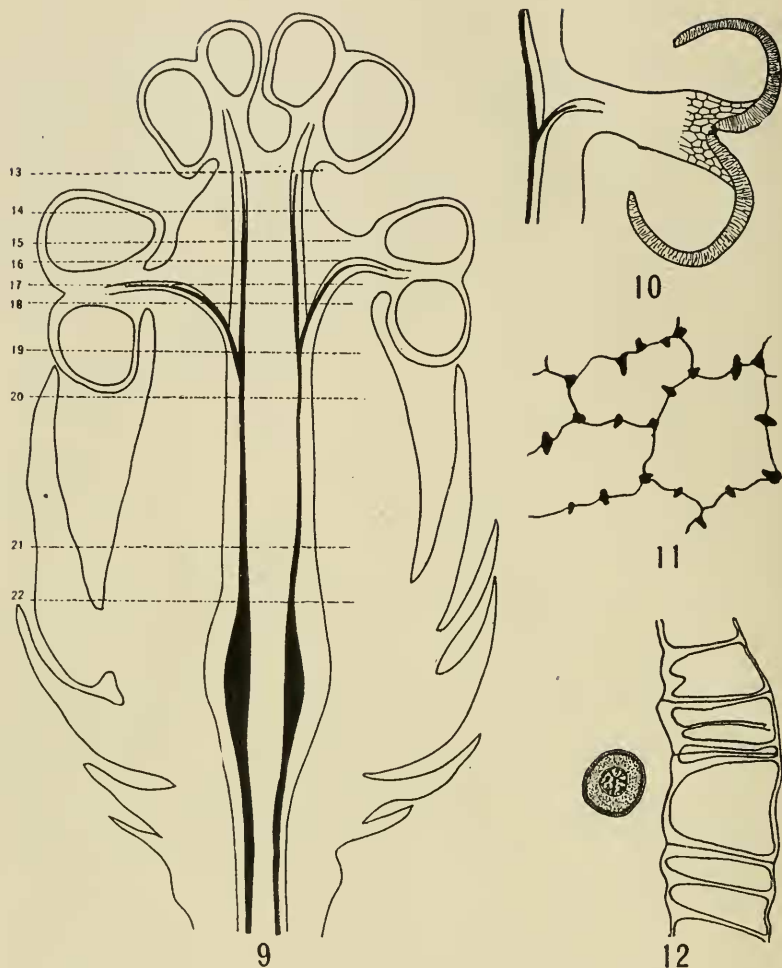
From the beginning of the primordium to the mature sporophyll the epidermis remains as a distinct layer, the sporangium developing from hypodermal tissues, as already stated. During the early growth of the sporophyll the epidermis is meristematic throughout, dividing anticlinally (fig. 24), its surface area thus keeping pace with the increase in the mass of the sporogenous tissue. An occasional periclinal division results in the epidermis becoming 2 cells thick at

some points. The meristematic ability, however, soon becomes limited to the base of the sporangium, the epidermal cells of the remainder of the sporophyll becoming larger and with less dense contents, the cells at the base remaining isodiametric and rich in cytoplasm (figs. 32-34). As the sporangium increases in size, causing a more pronounced lobing of the sporophyll, the necessary increase in epidermal surface is effected by the enlargement of the non-meristematic cells and the addition to them of cells from the basal meristematic region. The enlarged cells become filled with an amorphous substance and the walls become thicker.

By the time the sporangia are mature the epidermis has become the functional wall of the sporangium, owing to the practical disintegration of the true sporangium wall. At maturity the epidermal cells are devoid of contents and have the markings characteristic of the walls of many sporangia (figs. 11-12), these thickenings exercising a hygroscopic effect, useful in the liberation of the spores. JEFFREY (12) regards this thickening of the epidermal cells of the sporophyll, in a mechanical dehiscing device, as the result of the invasion of the epidermis by mechanical tissues of fibrovascular origin. There are no indications in *Taxus* of mechanical elements elsewhere in the sporophyll. COULTER and LAND found numerous stomata in the epidermis of *Torreya*. In *Taxus canadensis* there is a single stoma on a sporophyll, at the center of the peltate disk, occupying the bottom of the depression caused by the enlarged sporangia (fig. 10). GOEBEL (10) shows a similar situation in *T. baccata*.

Mature strobilus

The scales at the base of the strobilus are small and decussate, increasing in size and becoming spiral in arrangement above, the uppermost ones being considerably larger than the lower ones, and function as bud scales in the immature condition of the strobilus. The scales are brownish in color, with heavily cutinized outer epidermal walls, especially on the abaxial surface, the stomata occurring only on the inner surface (fig. 37), reversing the condition on the vegetative leaves of the plant, where the stomata occur only on the lower (abaxial) surface. The midrib is marked by the



FIGS. 9-12.—Fig. 9, median longitudinal section of mature strobilus just before pollen shedding, showing “elongating region” of axis and 4 sporophylls; xylem of bundle black; note that xylem becomes centrally placed in upper portions and does not extend as far into stalks as phloem; numbers at left (13-22) indicate approximately levels of cross-sections of strobilus shown in figs. 13-22; fig. 10, median section of open sporophyll, showing elongated stalk, open sporangia, and solitary stoma in center of depression of disk; fig. 11, tangential section of mature epidermis, showing mechanical thickenings on walls; fig. 12, cross-section of mature epidermis, with microspore, at time of shedding; figs. 9, 10, $\times 36$; figs. 11, 12, $\times 475$.

vascular bundle, when present, and occasionally by sclerenchyma-like cells along the outer margin of the midrib. In the young strobilus the mesophyll of the scale is compact, but as the strobilus matures large air spaces develop. In addition to the solitary stoma found on the sporophyll, stomata occur on the strobilus axis between the bases of the sporophylls with rather surprising frequency, being found only on this portion of the axis and not on the portion between the upper scales and the lower sporophylls. While the functional character of these stomata might be open to question, owing to their position rather than to their structure, their chief interest probably lies in their morphological significance as hereditary structures from a more highly vegetative ancestral strobilus.

During the autumn, winter, and early spring the strobilus has the appearance of a globular "bud," the stamens being surrounded by the uppermost scales (fig. 7). The axis between the upper scales and the bases of the lower sporophylls is very short and remains so until a few days before maturity, during the latter part of April in central Pennsylvania, at which time there is a rapid enlargement and elongation of this portion of the strobilus, the effect being to push the sporophyll-bearing portion beyond the scales (fig. 9). A similar elongation of this region is reported for *Torreya californica* (20). COULTER and LAND described an enlarged pith region in the axis of the strobilus in *T. taxifolia*, which the authors suggest may be "an important storage region for the strobilus." No such enlarged region was found in *T. canadensis*. In addition to the elongation of this portion of the strobilus axis there is also an elongation of the stalk of the sporophyll (cf. figs. 9 and 10), resulting in the separation of the sporophylls from one another.

The sporangia do not hang freely from the underside of the disk, but are fused with the stalk on the inner side (fig. 9), and laterally are separated from one another only by thin partitions, the external furrows between the sporangia not extending all the way to the center, the sporophyll and sporangia thus constituting a very compact structure. RICHARD (19), STRASBURGER (22), and GOEBEL (10) gave accounts of the dehiscence of the sporangium of *T. baccata*, in which they pointed out the rupture of the sporangia at the base and the umbrella-like movement of the epidermal wall.

The process is the same in *T. canadensis*, the breaking of the thin-walled epidermal cells at the base of the sporangium in a circle around the base of the stalk, the rupture of some of the cells at the side of the sporangium, and the hygroscopic rôle of the thickened epidermal cells resulting in the wall of the sporangia spreading out in umbrella form, the thin partitions between the several sporangia also being broken in the process.

When young the strobili rudiments are erect in the axils of the leaves, but as they develop they become oriented in such a way as to hang pendent on the lower side of the shoot, the fertile portion of the strobilus being directed downward. GOEBEL (10) regards the position and the method of dehiscence such as to secure the most advantageous distribution of the pollen.

Vascular features

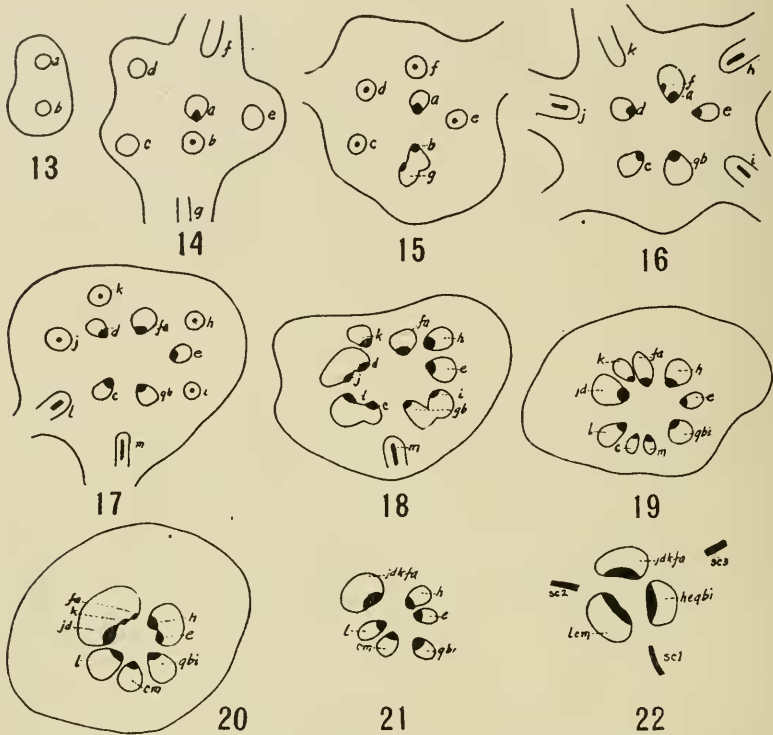
Since the reproductive organs, and especially the staminate structures, are regarded as among the most conservative of plant organs, a consideration of the vascular anatomy of the staminate strobilus is not without interest. While the ovulate strobili of conifers have been the subject of considerable investigation and discussion, in their vascular as well as in other features, the staminate strobili have not received much attention in their vascular anatomy, probably not as much as they deserve in view of the conservative nature generally assigned to them on other grounds. The only reference to this feature of *Taxus* is by STRASBURGER (22), who gave the arrangement of the scales of *T. baccata* and states that each stamen contains a bundle which passes into the stalk.

Like any other branch, the strobilus axis receives 2 bundles from the cylinder of the leafy shoot. These are semicircular in outline, and by meeting at their edges soon form a closed cylinder, broken here and there by the gaps formed by the weak bundle traces of the scales. In the lower portion of the strobilus, where the scales are small and decussate, the small traces often end in the cortex and do not reach the scale itself. The traces for the upper scales are better developed and extend for some distance into the midrib of the scale, especially in the 2 or 3 uppermost scales. Although the axis cylinder, as well as the cortical portion of the scale traces, are

collateral endarch, in their terminal portions they contain not only centripetal xylem, but are also accompanied by transfusion tissue which may be both dorsal and lateral to the xylem elements (fig. 38).

At the level of the uppermost scales the cylinder consists of 3 or 4 large bundles (figs. 22, 48) which extend into the fertile portion of the strobilus, where they branch, giving off finally a branch to each sporophyll, the bundle extending a little way into the base of the sporophyll stalk. In a young strobilus these bundles are represented only by elongated thin-walled elements, evidently procambium strands, which traverse the region between the base of the sporophylls and the level of the upper scales (figs. 7, 8). These strands remain in this embryonic condition until near maturity, when they elongate and take on their vascular features in connection with the growth of the "elongating region" of the strobilus axis. In this "elongating region" the pith becomes larger in diameter than in the lower portion of the strobilus, but shows no evidence of being in any way a storage region; in fact, there would be little use of a storage tissue at this stage in the development of the strobilus. The several large bundles of the strobilus axis extend for some distance into the "elongating region" and then give off branches to the various sporophylls, each of the large bundles supplying several sporophylls in this way (figs. 13-22). Some of the branches may unite and then separate (see the behavior of bundles *h* and *e*, and also of *l*, *c*, and *m*, in figs. 18-22), although usually the bundles pass rather directly to the base of the sporophyll (figs. 14-17, 44-47). Throughout the entire axis there is relatively a stronger development of the phloem than of the xylem, the latter forming a narrower zone than the former (fig. 48). Both xylem and phloem reach their greatest development near the level of the upper scales (figs. 9, 22), above this the xylem forming only a very narrow portion of the bundle. Throughout the strobilus the xylem consists of spirally thickened tracheids with bordered pits, the tracheids being rather short, however, although in the elongated region of the axis they are somewhat longer than at a lower level and the bordered pits are fewer in number. The phloem of the portion above the scales shows very little of the pitting present at a lower level, consisting

of elongated cells similar to those of the younger condition of the strobilus. Occasionally the xylem extends a short distance into the stalk of the sporophyll, the bundle here, however, usually consisting



FIGS. 13-22.—Cross-sections of mature strobilus at approximately levels indicated by numbers to left of strobilus shown in fig. 9; branches of bundles to various sporophylls indicated by *a, b, c*, etc., xylem indicated by black; bundles *a* and *b* supply terminal sporophylls; union of bundles indicated by combining letters, as *jd* in figs. 17-19; fig. 19 shows complete cylinder below lowermost sporophyll; in fig. 18 *l* and *c* united, in fig. 19 separated, in fig. 20 *c* and *m* united, and in fig. 22 *lcm* one of the 3 large strands from sterile portion of axis; fig. 22 also shows traces to 3 uppermost scales, *sc1*, *sc2*, and *sc3*; note concentric character of terminal portions, as in *c, d*, and *e*, in fig. 15; $\times 36$.

only of the phloem portion (fig. 39), the xylem usually ending within the cortex of the axis.

The bundles of this region are collateral endarch in the lower portions. In the upper portions, however, the bundles frequently show centripetal xylem (figs. 40, 44), giving mesarch bundles, and

in some cases the smaller xylem elements are on the outside of the bundle, indicating a possibility of exarch structure (fig. 42). In addition, the xylem elements, in the terminal portions of the bundles, become more and more placed toward the center of the bundle, giving virtually a concentric bundle of a few xylem cells surrounded by the phloem portion of the bundle (fig. 41). No transfusion tissue was found elsewhere than in the scales.

Discussion

Perhaps the two most important features of the staminate strobilus of *Taxus* are the peltate sporophylls and the character of the vascular bundles of the scale and sporophylls. The peltate (epaulet) type of stamen occurred among the Paleozoic Cycadofilicales, in the *Crossotheca* forms, but the sporangia were bilocular and dehisced by a longitudinal slit along the adaxial face, the bilocular character being different from that of the modern gymnosperms. Peltate stamens are not known in Bennettitales, and none occur in the Cycadales. The peltate stamen has been carried forward to modern plants through the Cordaitalean line, in all probability, although so far as is known the stamens in the Cordaitales bore terminal erect sporangia. As COULTER and CHAMBERLAIN state, however, "it cannot be supposed that the stamens of so great a group were uniform in type," and it is very possible that peltate stamens occurred there also. The sporophyll of *Ginkgo* gives a suggestion of the peltate type of stamen, in occasionally having more than 2 sporangia, in the regular occurrence of more than 2 sporangia in fossil forms, and in the possibility, pointed out by Miss STARR, that the mucilage cavity replaces abortive sporangia. Among Coniferales there is a suggestion of the peltate stamen in the Araucarineae, and stamens of true peltate form occur in such forms as *Widdringtonia*, *Torreya*, and *Taxus*. In *Torreya* the true peltate character is generally obscured in the adult sporophyll owing to the development of the resin cavity from 3 of the 7 sporangium beginnings. Hence it is seen that peltate stamens, in one form or another, are scattered from Cycadofilicales to modern conifers, and there is no necessity of regarding such a sporophyll as that of *Taxus* as being of recent evolution. Assuming peltate

sporophylls in Cordaitales as probable, their continuation in Ginkgoales and Coniferales is quite possible, abortion of some of the sporangia in the formation of mucilage or resin cavities, in such forms as *Ginkgo* and *Torreya*, obscuring their true nature, but showing the true peltate character when all of the sporangia develop, as in *Taxus*. WORSDELL, following the view put forward by CELAKOVSKY (2), considers the peltate sporophyll of *Taxus* to have been derived from such a form as occurs in the Cordaitales, where the pollen sacs are "erect and terminal on the radial sporophyll," through such forms as found in *Cephalotaxus* and *Torreya*, where the pollen sacs are "sub-terminal and pendulous, owing to a slight prolongation of the axis of the sporophyll, between and beyond the sacs, in a small protuberance," this condition being intermediate between the Cordaitales situation and *Taxus*, "where the extended terminal portion has become enlarged and flattened out into a very distinct peltate structure." "*Taxus* thus represents an advance from the earlier types of *Cephalotaxus*, *Ginkgo*, etc., toward the subpeltate dorsiventral type of sporophyll of the true Coniferae." One must question the necessity of such an explanation for either the peltate sporophyll of the taxads or the dorsiventral one of most conifers, in view of the historical occurrence of both of these types in forms more primitive than even the Cordaitales.

The significant features of the vascular anatomy of the strobilus are the mesarch character of the terminal portion of the scale bundles, as well as the appearance of centripetal xylem in the terminal portion of the sporophyll bundle, where the bundle is not only mesarch at times, but may also be exarch and concentric. This indicates the very conservative nature of the staminate strobilus. These primitive features, however, occur only in the terminal portions of the strobilus, which may be regarded as an argument in favor of the "advanced" character of *Taxus*, compared with forms with more abundant centripetal xylem.

Summary

1. The staminate strobili occur in the axils of the leaves. The buds can first be distinguished from other types of buds by the broad apex.

2. The sporophyll primordia first appear as slightly rounded lobes above the general surface and may arise in acropetal succession.

3. The archesporial initials are hypodermal cells and develop according to the eusporangiate method. There are 4-8 of them, distributed around the margin of the primordium.

4. The sporogenous tissue reaches the mother cell stage about October 1, and forms microspores about 2 weeks later. There is no abortion of sporangia such as occurs in *Torreya*, the sporangia occurring in a circle around the stalk of the sporophyll.

5. The sporangium wall is usually 2-layered. The tapetum arises from the peripheral layer of the sporogenous tissue and persists until after megaspore formation.

6. The epidermis of the sporangium remains alive and thin-walled at the base, dehiscence being accomplished by the rupture of these cells at maturity, by the elongation of the stalk of the sporophyll. Owing to the disintegration of the sporangium wall, the epidermis is the functional wall in the later stages.

7. The strobilus matures the latter part of April. Just before maturity there is an enlargement and elongation of the axis, pushing the sporophylls beyond the scales.

8. The strobili of *Taxus canadensis* are somewhat smaller than those of *T. baccata*.

9. The strobilus bundles are collateral endarch, excepting in the terminal portions of the scale bundles and the sporophyll bundles, where they may be mesarch, and in the latter show indications of occasional exarch structure, the terminal portion of these bundles also being concentric.

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EXPLANATION OF PLATES XXIV—XXVI.

All drawings were made with a camera lucida; text figs. 1-10 and 13-22 are drawn to the same scale, with a magnification in reproduction of approximately 36; text figs. 11-12 and all plate figs. are drawn to the same scale, reduced one-half in reproduction, having a magnification of approximately 475.

PLATE XXIV

FIG. 23.—Young sporophyll primordium, showing 2 archesporial initials in hypodermal layer of rounded primordium.

FIG. 24.—Archesporial initial in hypoderm; division of epidermal cell.

FIG. 25.—Archesporial initial in tangential section.

FIG. 26.—Archesporium of 2 cells.

FIG. 27.—Metaphase in division of archesporial initial.

FIG. 28.—Late stage in division of archesporial initial.

FIG. 29.—Primary wall cell (outer cell) and primary sporogenous cell (inner cell), resulting from division of initial.

FIG. 30.—Primary wall cell and division of primary sporogenous cell.

FIG. 31.—Primary wall cell has formed 2 tiers of wall cells, in one of which division is taking place; primary sporogenous cell has divided anticlinally, forming 2 sporogenous cells.

FIG. 32.—Lobe of young sporophyll, showing small mass of sporogenous tissue, 2-layered sporangium wall formed on outer side, and meristematic basal portion of epidermis differentiated from remainder of epidermis.

FIG. 33.—Somewhat older stage than fig. 32.

FIG. 34.—Sporangium wall complete, entirely surrounding sporogenous mass; latter part of July.

FIG. 35.—Older sporangium, showing differentiation of tapetum from sporogenous tissue.

FIG. 36.—Portion of sporophyll, showing epidermis, 2-layered sporangium wall with narrow flat cells, tapetum (1 cell binucleate), and microspores; winter condition.

PLATE XXV

FIG. 37.—Transverse section of portion of lower scale, showing stoma on inner surface and heavily cutinized epidermal walls, especially on outer surface.

FIG. 38.—Transverse section of portion of upper scale, showing vascular bundle and inner epidermis of scale; in vascular bundle note centripetal xylem and 2 transfusion cells, 1 dorsal, 1 lateral to xylem.

FIG. 39.—Transverse section of bundle *a* of fig. 13, showing phloem character of bundle; no xylem present.

FIG. 40.—Bundle *a* at level of fig. 15, showing mesarch character.

FIG. 41.—Bundle *e* of fig. 15; single xylem cell surrounded by phloem.

FIG. 42.—Bundle *e* at a lower level; large xylem cell centripetal to smaller ones, indicating possible exarch condition.

FIG. 43.—Bundle *gb* at level of fig. 17, showing collateral endarch character.

PLATE XXVI

FIGS. 44-47.—Fusion of bundles *f* and *a* (see figs. 15-17): in fig. 44 *f* is concentric, *a*, mesarch collateral; section 60 μ below level of fig. 15; fig. 45, enlarged view of bundle *fa* of fig. 16, 80 μ below fig. 44; fig. 46, 2 bundles near together 20 μ below fig. 45; fig. 47, fusion bundle *fa* 30 μ below fig. 46.

FIG. 48.—Transverse section of bundle *lcm* near level of fig. 22.